

## THE IMPACT OF VERTEBRATE PREDATORS ON EARLY ARTHROPOD EVOLUTION

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*Abstract.*—The extinctions of several “orders” of insects near the close of the Paleozoic resulted from increasingly effective predation by visually hunting tetrapods. Forms living on the surface of the ground were the first to be affected. The larger immatures of the early Pterygota were especially vulnerable because they could not yet fly, nor could they enter crevices easily because they were encumbered with large, laterally projecting wing pads. Surviving “orders” had immatures capable of avoiding diurnal tetrapod predators. Some immatures escaped by living in water (Ephemeroptera, Odonata, Plecoptera); some hid in crevices during the day (Blattodea, Coleoptera, etc.), or were too small to be attractive as prey (Collembola, Psocoptera). Endopterygote larvae lived out of sight in soil litter; mecopteroid larvae lived there permanently, neuropteroid larvae hid there during the day, but foraged above ground at night.

Intrinsic advantages in exploiting divergent larval and adult habitats did not induce the complete metamorphosis of endopterygotes; vertebrate predators coerced the divergence between larval and adult modes of life. The adaptive radiation of the Endopterygota also did not result from direct competitive advantages of their metamorphosis. The larvae simply moved into new niches created directly or indirectly by the adaptive radiations of vascular plants. There were probably no fewer exposed niches for exopterygotes, but tetrapod predators severely restricted the exploitation of those niches.

The neopterous wing-flexing mechanism was originally an adaptation for settling into open crevices. It eliminated the silhouette that revealed the insect's position, especially on tree trunks. It was evidently very effective until beaked birds began fishing insects from crevices.

Aerial predation by Odonata and Protodonata deterred early insects from flying freely during the day. For this reason the adults of most orders came to rely primarily on means other than flight to escape tetrapods.

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Early terrestrial arthropods played an indispensable role in the origin and early evolution of terrestrial vertebrates: they were the food that sustained vertebrates as they became terrestrial. Apparently, only the Arthropoda developed terrestrial populations sufficiently large to support the widescale adaptive radiations that occurred among the early terrestrial vertebrates. Terrestrial vertebrate herbivores, capable of supporting

significant populations of vertebrate predators, did not appear until the Permian. Indeed, the rapid evolutionary expansion of early reptiles seems to have occurred primarily in response to the rapid increase in numbers and kinds of insects (Olson, 1976). Many later adaptive radiations among terrestrial vertebrates similarly appear to have depended on an “insect” food base (Rohdendorf, 1970).

The earliest known terrestrial vertebrates were found in Carboniferous deposits. Their dentition consisted of small, sharp-pointed teeth. Since such teeth generally function in seizing small arthropod prey and swallowing them whole in modern species, then the early terrestrial vertebrates must have been similarly "insectivorous" (Carroll, 1982; Gregory, 1950; Olson, 1976; Milner, 1980).

The preceding ideas have been widely accepted, and are not in question here. The references cited provide access to additional discussion on this matter.

#### MISSING HYPOTHESES

The early dependence of terrestrial vertebrates upon arthropods has not lacked in interest, nor was the idea suggested only recently. But, curiously, the reciprocal impact of early tetrapods on insects and their relatives has never received comparable attention. The primary focus has almost invariably been on vertebrate evolution, although Rolfe (1980) made several references to possible coevolutionary relationships between tetrapods and terrestrial or amphibious arthropods, and Kukulova-Peck (1978) spelled out a number of significant but seldom mentioned features of Paleozoic insects, considered mainly in relation to wing evolution and metamorphosis.

Obviously, the advent of reptiles was a critical development for terrestrial arthropods. The reptiles were not a minor group, and terrestrial arthropods were their main food. It is inconceivable that early terrestrial vertebrate predators did not seriously affect the course of arthropod evolution on land.

The purpose of this paper is to point out that the extinctions of the Palaeodictyoptera and several comparable "orders" of insects in the late Paleozoic resulted from early vertebrate predation. Further, many conspicuous features of the surviving arthropod orders were shaped originally, and have continued to be shaped, in no small measure by terrestrial vertebrate predators.

These hypotheses and their derivatives differ from previous considerations in that they do not have vertebrate evolution as their subject; they concern particular changes that occurred among early arthropods as a result of terrestrial vertebrate predation. Extinction, of course, is one of the more significant and drastic changes.

#### SOURCES OF THE EXPLANATIONS

The ideas presented here are hypotheses extrapolated from published ideas or ideas stemming from common field observations of modern species. The key hypothesis derives (in part) from the following: vertebrates (presumably birds foremost, but also lizards and diurnal amphibia) have had a staggering impact on insects in the tropics. Elton (1973) reported finding widespread feeding damage on the foliage of Neotropical trees, but, paradoxically, virtually no sign during the day of any insect that could have caused the damage. Evidently, neither cryptic nor warning coloration nor any ordinary escape mechanisms provide sufficient protection under the highly competitive conditions of the tropics. The insects have resorted to hiding physically from their vertebrate predators during the day.

Adaptive coloration in insects is one of the strongest indications of the profound impact of visually-hunting vertebrate predators. All insects of any size exposed during the day are colored. This is so obvious that it is seldom mentioned—in such general terms. Yet, the fact that cave insects, fly maggots, certain beetle larvae, etc., all of which lead continuously concealed lives, are not colored points to the all-pervasive effect of visually-hunting vertebrate predators. The arthropod compound eye is not known to provide sufficient visual acuity to account for the elaborate colors and structural patterns of contemporary insects, which leaves vertebrates as the primary selective agents for most of these patterns.

Some coloration is not related to verte-

brate predation, such as that employed in courtship or heat regulation or the blacks or browns incidental to strong sclerotizations. None of these (as color patterns) are as prevalent or basic among insects as cryptic or aposematic patterns that relate to vertebrate predation.

The eye-spot patterns on the wings of certain Paleozoic insects (Carpenter, 1971) suggests that the use of color patterns in insects as a response to tetrapod predators was determined that long ago, no doubt largely by the fundamental structure and capabilities of the vertebrate eye and brain. According to Blest (1957), the eye-spot patterns of Lepidoptera wings may serve two functions: 1) they may simulate a larger predator and so frighten off an attacker. or 2) they may, as a salient target, deflect an attack to a less vulnerable part of the lepidopteran body. The last, presumably, deflects bird pecks from the vulnerable body to the less vulnerable wing extremities. In either case, eye spots function as defenses against vertebrate attack. But birds did not exist in the Paleozoic!

#### EXTINCTION BY VERTEBRATE PREDATION

It is not possible to say exactly when any major type of terrestrial arthropod became extinct. The fossil record does not reveal when the last palaeodictyopteran disappeared from the earth. Nevertheless, certain groups occur regularly up to a certain point, but are consistently absent from later deposits. There is always the possibility that the early and later deposits are not equivalent, and that later representatives simply were not fossilized. However, the total absence of Palaeodictyoptera and various other orders from all records after the Permian indicates that a major change had taken place, whether catastrophic or gradual, even if this change was completed in the Triassic. For the purposes of this paper, such disappearances from the record are treated simply as extinctions. If some relicts lasted

much longer than they appear to have from the fossil record, it is of little consequence for the hypotheses developed here.

The hypothesis that early vertebrate predators reduced populations of certain types of insects, such as the Palaeodictyoptera, but not others, to the point of extinction accords far better than any alternatives with conventional evolutionary thought and the data of the fossil record. As already mentioned, tetrapods began by eating terrestrial arthropods. It is unreasonable to assume that terrestrial arthropods were unaffected, since vertebrates were becoming increasingly numerous and better adapted for life on land. Moreover, the extinction of major arthropod types correlates in geological time with the early adaptive radiations among terrestrial vertebrates, the reptiles in particular.

Vertebrates are (and were) normally larger than their arthropod prey—in vertebrate-arthropod encounters it is the arthropod that would ordinarily end up as prey. While some mammals are nocturnal insectivores, the early tetrapods appear to have been diurnal and visually oriented hunters.

Conceivably, arthropods and their tetrapod predators might enter into coevolutionary progressions without major extinctions. No doubt many did. However, extinctions are possible under certain conditions. For example, New Zealand mayflies evolved in streams in which they were safe from predatory fish. Their immature stages lived an exposed life, and did not hide like their relatives in the rest of the world. Some swam freely through open water. Trout, introduced early in this century, ate them in such numbers that in 20 years the once extremely abundant mayflies had become rare if not extinct (Tillyard, 1926; Burks, 1953).

It does not matter that the New Zealand mayflies may not be completely extinct. The drastic reduction in their numbers effectively removed their evolutionary potential in New Zealand from them. The Paleozoic

tetrapods are equivalent to the trout in New Zealand.

#### EXTINCTIONS: ALTERNATIVE EXPLANATIONS

A few alternative explanations have been suggested for the early arthropod extinctions. Major climatic changes, a large meteorite impact, or simple replacements by more efficient types have usually been regarded as the more plausible. Climatic changes in combination with replacements by new types have been suggested as the primary cause of the late Paleozoic extinctions (Ross, 1965, for example). Hennig (1981) suggested essentially the same idea, but emphasized replacements by more vigorous types of insects.

The Permian has been characterized as a time of tectonic upheaval and great climatic change. It has been called "a crisis point in the history of life" (Schuchert and Dunbar, 1941). Both Newell (1982) and Raup (1979) discuss the peak of extinctions of major groups that occurred near the end of the Permian. This is superficially consistent with the idea that climatic changes were responsible for the extinctions of various arthropod groups, which were replaced by more adaptable types later on.

However, the Appalachian Revolution with its widespread uplifts and more varied, drier climates did not abruptly terminate the Permian Period. The Revolution began with and continued during the Period (Colbert, 1980). In such case the extinctions ought to have occurred mainly at the beginning of the Permian when arthropods would have been most seriously stressed in their first encounters with the new climates.

On the contrary, Carpenter (1977) pointed out that the Permian insect fauna was obviously much more diverse than the Pennsylvanian—"In terms of diversity of form and the association of generalized and specialized species, the fauna of the Permian was probably the most diverse in the history of the Insecta." If anything, the widespread uplift with the increased diver-

sity of climates and habitats had an effect opposite to the one called for: it seems to have been more effective in producing new orders and adaptive radiations rather than extinctions among arthropods. Later tectonic upheavals and the accompanying climatic changes also do not seem to have produced comparable major extinctions among arthropods as, for example, during the Laramide Revolution at the end of the Mesozoic. The latter revolution is as much associated with adaptive radiations as with extinctions. From these considerations alone there is no reason to assume that any ordinary climatic changes caused the late Paleozoic arthropod extinctions.

A serious drawback to the climatic change hypothesis is that it is extremely vague. Exactly how did Permian climatic changes affect the evolution of any given species or group? Most of the known insect fossils are from only a few tropical swamp forest deposits, although some are from temperate deposits (Wootton, 1981). And for what reason would one order, such as the Palaeodictyoptera, be affected disastrously by climatic changes, but not another, such as the Blattodea. In its present loose formulation the climatic change hypothesis does not permit deducing accurate enough consequences to permit practical observational tests.

More plausibly, extinctions might have resulted from a climatic disaster as might have been caused by a large meteorite impact. This has been suggested as the reason for the extinctions of the dinosaurs at the close of the Mesozoic (Alvarez et al., 1982, is a general consideration of this topic and is part of a major symposium on the subject, q.v.). This proposal has the advantage of yielding several precise consequences which are that the extinctions should be abrupt, extensive and synchronized, and that they should be followed by a slow recovery from an impoverished fauna.

The geological record for the closing period of the Paleozoic fits this pattern in some

respects: the later Permian mass extinction has been regarded as "the single most devastating collapse of the marine ecosystem" we know of (Sepkoski, 1982). Numerous extinctions appear to have occurred at that time (Raup, 1979).

However, the arthropod extinctions were not all simultaneous. Some occurred earlier or later (diagram in Smart and Hughes, 1973). Most of the extinctions were not sudden (Tappan, 1982). Further, the record of the extinctions is essentially a marine record. There are few fossils of terrestrial arthropods to compare from the early Triassic; the apparently synchronous extinctions of several major arthropod groups near the close of the Permian might be an artifact of the fossil record. What evidence there is, including much from the vertebrate record, "makes a catastrophic event at the end of Permian time difficult to support" (Olson, 1982) (speaking of terrestrial environments). No one has been able to confirm an iridium anomaly near the end of the Permian (Silver, 1982; the iridium anomaly has been interpreted as a result of a major meteorite impact in the Cretaceous).

But could the extinctions reflect replacements by better adapted types, as Hennig (1981) seems to favor? At least from the standpoint of major types of insects, there does not appear to be any support for this view either. Which order supplanted the Palaeodictyoptera (or any other group), or which order was transformed into the Diptera (or any other order)? Virtually none of the relevant major phylogenetic questions have been answered (Wootton, 1981). Present information indicates that a number of orders of both insects and arachnids disappeared in the late Paleozoic with no known descendants and no recognizable replacements.

Another possibility is that the extinction of a major plant group would result in the extinctions of insect dependents. The difficulty with this hypothesis is that this presupposes that a major arthropod group was

entirely dependent on a particular plant group that then became extinct near the end of the Paleozoic. Some palaeodictyopteroid insects may have fed on the endosperm of paleozoic megaspores, but this is far from suggesting that all of them did, or that none were capable of evolving along with plants that survived. The extinction of the plant group itself would still beg explanation.

Tappan (1982) developed an interesting plant dependency hypothesis. She related the marine extinctions at the end of the Permian to the development of a more advanced land vegetation. The increased biomass and more extensive soils which accompanied this vegetation retained much of the nutrient material that formerly washed into the sea. Presumably this effect was exaggerated by the widespread uplift that seems to have characterized the Permian (because it resulted in a more extensive terrestrial vegetation). As a result, the marine phytoplankton became increasingly starved, and eventually whole food chains collapsed.

The collapse of marine food chains, according to Tappan's hypotheses, does not entail a terrestrial catastrophe. They imply exactly the opposite: a greater development of terrestrial plant life and, presumably, an enriched arthropod evolution there. It should be pointed out, however, that a marine catastrophe of the magnitude recognized must surely have affected life on land to some degree. If nothing else, marine photosynthesis would probably have been affected, which is no minor matter. However, no one seems to have detailed such consequences, nor have any of the major terrestrial extinctions been related specifically to the marine catastrophe.

Another possibility is that predatory arachnids rather than vertebrates caused the major arthropod extinctions. This also is not plausible. The fossil record for terrestrial arthropods is very poor until the Carboniferous. At that point both arachnids and insect appear as rich coexisting faunas, which became more diverse together during the

Carboniferous and Permian (Savory, 1977). Major extinctions caused by arachnida must have occurred prior to the development of a significant fossil record, perhaps in the Devonian. The Devonian myriapods (Peach, 1889), Collembola (Scourfield, 1940), and arachnids (Rolfé, 1980) point to an earlier inland differentiation of which we have scant record. But, since we know so little, it is not possible to develop precise ideas about such early events.

Another possibility is to assume that there is no one explanation, but various unknown reasons for the extinctions. To take this position precludes developing precise explanations, and it leaves untouched the problem of why certain orders should become extinct rather than others. Why not some of each? The fact that it was not simply some of each, and that many of the extinctions occurred in the same general time period indicates that the extinctions were not random or "pseudo-random" but according to some pattern that affected certain arthropod types more seriously than others. Hence, general explanations should be possible.

#### A MODE OF LIFE PROBLEM

Schmalhausen (1957—discussed in Rohdendorf, 1970) argued for a view that is not compatible with the vertebrate predation hypothesis developed here. They suggested that the first terrestrial vertebrates were initially "passive," feeding on insects when the latter crawled into their mouths. Glandular areas in the amphibian mouth were evidently taken as the supporting evidence, apparently on the assumption that such glands must have been present originally because the "salivary" glands of contemporary amphibia must be derivatives of some such precursors. The glands were said to function in the "fixation" of the food insects.

While not mentioned by Rohdendorf, nocturnal habits might be regarded as likely for early amphibia becoming reptiles. Their moist skin would render them susceptible to desiccation; nocturnal habits would have

them active when relative humidities would ordinarily be higher than during the day. Nocturnal habits would not be especially conducive to active visual predation, and, hence, these ideas are more compatible with Schmalhausen's and Rohdendorf's ideas than with the hypotheses developed here.

But a host of implications have been ignored. There are simply no grounds for assuming that whatever glands may have been present functioned as sticky traps in propped-open mouths. Clamping the mouth shut should have "fixated" any ordinary insect prey. It is also difficult to conceive of any features of an aquatic ancestor that would predispose them or their amphibian descendants to such a mode of prey capture. That is, no origin or pathway can be pointed to that might lead to the situation depicted by Rohdendorf and Schmalhausen, and neither the hypothesis nor its implications are supported by any observational data I have been able to find. Had the first terrestrial vertebrates started as postulated, selection might be expected to have produced ever better methods of baiting and sticky-trapping. So far as we know, it produced neither; it produced active hunters. Neither fossil nor modern amphibian structures suggest the "passive" feeding hypothesized by Schmalhausen and Rohdendorf.

Even the nocturnal habits of modern Amphibia may not be primarily adaptations for avoiding desiccation. They are as easily explained as the result of predation by larger vertebrates. Frogs, which ambush insect prey and might be regarded as the closest modern approximation to the Schmalhausen prototype, depend on their comparatively large eyes for prey capture; these indicate earlier diurnal habits. The highly poisonous harlequin frogs (*Bufo*idae) of Central America are neither retiring nor nocturnal (Martha L. Crump, personal communication, 1985); but they are apparently too poisonous to be attractive as prey for most predators.

By way of contrast, the simplest transition from an aquatic life to one on land entails

supposing only that certain amphibians moved from seizing prey and swallowing it whole in water to doing the same on land, as their teeth suggest. This is a direct, simple and obvious pathway that began with nascent amphibia making temporary forays onto land for insect prey. It implies active searching rather than passive trapping, which is consistent with the continued development of eyes and legs in the subsequent adaptive radiations of terrestrial vertebrates. The eyespot patterns on the wings of a Paleozoic insect (Carpenter, 1971) make little sense, except in the context of visually hunting tetrapods.

#### OBSERVATIONAL TESTS OF THE THEORY

The vertebrate-predation hypothesis developed here, when conjoined with various generally accepted or fairly obvious ideas, yields numerous implications (deductions or predictions) that fit available observational data extremely well. Several examples are discussed below.

The earliest vertebrate incursions into the terrestrial arthropod world probably began in the Devonian in the vicinity of bodies of water where the early vertebrates lived. As mentioned above, the habit of seizing prey and swallowing it whole would suffice for prey capture on land as well as in water. No major structural or behavioral changes would be called for aside from those related to coping with the physical problems of an aquatic animal attempting to live on land. The essentially untapped terrestrial arthropod fauna would have been a major enticement for the earliest tetrapods to forage there, and no comparable predators had preempted their predatory role on land. The arachnids were not equivalent competitors, since the tetrapods could eat them also.

The vertebrate emergence from water onto land was no minor transition, since virtually every organ system would need to be reorganized for the vastly different conditions of life out of water. Consequently, the first amphibian tetrapods must have been com-

paratively inefficient and clumsy predators on land; their impact on arthropods must have been minimal until reptiles more fully adapted for life on land evolved. At that point, it would no longer be safe for arthropods to roam freely over the surface of the ground during the day; arthropods active on the ground surface would be especially vulnerable to early reptilian predation.

In general, sensory-nervous mechanisms are slow to evolve (Smith, 1952), apparently because of their extreme complexity. Accordingly, we should expect the early terrestrial arthropods to be limited to relatively simple mechanisms for avoiding vertebrate predation. The following seem most likely:

- 1) The early arthropods might not "respond" at all, but simply succumb to vertebrate predation and become extinct.
- 2) They might avoid vertebrates, as by crawling out of sight into the soil litter.
- 3) They might become too small to be attractive as prey.
- 4) They might evade predators by jumping.
- 5) They might utilize distinctive color patterns to frighten vertebrates (the eyespots mentioned above).
- 6) They might develop noxious substances.
- 7) They might survive by living up on tree trunks out of reach of the early vertebrates rather than on the ground.

The last, a variant of option 2, may not be obvious. Tetrapod surface gaits are not suitable for climbing trees; for them, tree climbing requires the evolution of considerable "eye-hand" coordination, that is, it requires new, well-coordinated sensory-neural-muscular mechanisms that primitive tetrapods would not have had time to develop. Climbing otherwise would be hazardous, since falls from any height would injure animals of their size. Fossils of the earliest land vertebrates do not show adaptations for tree-climbing, as would be expected, although insectivorous, gliding rep-

tiles appear in the Upper Permian (Evans, 1982).

Insects and myriapods could climb easily because of their clawed legs and small size. Falls pose little threat, even to wingless insects, since most reach a low terminal velocity so quickly, that they are rarely injured in a fall, regardless of height. Epiphytic algae, fungi and lichens would enable them to feed on tree trunks as readily as on the ground.

From this it follows that some early arthropods living on tree trunks would survive early tetrapod predation longer than ground-surface species. Winged insects would best fit the epiphytic mode of life, since their adults could move the species between trees or stands (which would give easier access to their food and enable them to maintain larger outcrossing populations so important for their evolution). But trunk-dwelling arthropods would eventually face the same basic problems their predecessors had faced earlier on the ground. Simply climbing and feeding on tree trunks would, accordingly, be of only temporary utility, and epiphytic insects would eventually be limited to the first six options.

In summary, we should predict that forms dwelling on the surface of the ground would be the first to disappear (if of sufficient size to be attractive prey) followed by those that lived on tree trunks. As a corollary, all surviving groups should exemplify one or more of the first six responses to predators, as listed above. These predictions are realized abundantly among tracheates.

Example 1.—The recent and Paleozoic diplopod faunas do not resemble each other (Kraus, 1974). For this reason it had been assumed that the Paleozoic diplopods must not be closely related to modern groups. But, as Kraus pointed out, the modern classification is based on characters seldom preserved in Paleozoic forms, and there is good reason for believing that at least some modern diplopod groups have ancient roots.

Significantly, the conspicuous differences

between modern and Paleozoic diplopods relate to mode of life: the large eyes, long bifurcated spines, etc., indicate that the Paleozoic forms lived exposed on surfaces, perhaps on plants. The large eyes suggest diurnal habits. The majority of modern Diplopoda live below the soil surface, at least during the day. Is it an accident that the conspicuous differences between Paleozoic and modern millipedes are precisely those that would result from the elimination of surface-dwelling species by vertebrate predators?

Example 2.—Manton (1965) pointed out that the long-legged house centipede, *Scutigera*, appears never to have been adapted for burrowing or for living in shallow crevices, as have most modern centipedes. Further, it and its long-legged relatives have compound eyes. Obviously, the Chilopoda, like the Diplopoda, were not originally burrowers; they were adapted for a life on surfaces where their long legs and compound eyes were functional. Such a mode of life has not been open to them since the Paleozoic, and only the hidden burrowers and a few retiring scutigermorphs have survived, which is again readily explained as a consequence of predation by visually hunting terrestrial predators.

Example 3.—The Collembola do not provide compelling data, but the available data are in accord with the hypotheses as presented. They jump, and they are too small to be attractive prey to most vertebrate predators. Jumping does not make sense in confined spaces, and the more deeply "burrowing" species usually lose the furcula and become white. This group was obviously adapted originally for a surface life, and this is supported by the elaborate color patterns of many species.

Interestingly enough, some earlier Collembola were much larger than the species we are familiar with. Matthew (1895) described a collembolan from the "Little River Group" of New Brunswick, a deposit identified as either Silurian or Devonian by



Wilmarth (1938). This animal had an abdomen of "about" seven segments, and a strong "spring," but it was 20 mm long—large enough to be attractive prey for an insectivorous tetrapod. No Collembola this large have survived.

Example 4.—A rather involved body of theory indicates that Symphyla and Diplura were also originally surface-dwellers, but the account is too lengthy to develop here. It can be pointed out, though, that their relatively long, many-segmented antennae are incongruous with a burrowing life in the soil. Both groups appear to be crawlers-in-small-spaces, and, according to Scheller (1982), the Symphyla are incapable of burrowing.

Example 5.—Individuals of some species became so small as to be hard to see and perhaps too small to be worth chasing by most vertebrate predators. The Collembola exemplify this response on the ground; the Psocoptera exemplify it on tree trunks. So do the lice orders, although only derivatively. The Hemiptera and Homoptera probably also belong in this class, although less obviously. I postulate this: the hemipteroid precursors became small, so small that their jaws (especially in their early instars) could no longer gape widely enough for effective biting of the now relatively larger plant cells. It became easier to puncture plant cells and suck out the contents. These are the circumstances that would select for stylet-like mouthparts. It is the obvious pathway to entognathy. This explains the small size of the entognaths (in a functional, not a phyletic sense, to include tardigrades, Symphyla, Collembola, Diplura, Thysanoptera, and, incipiently, the Psocoptera).

Once an entognathous mode of feeding developed, it is conceivable that an insect might retain piercing mouthparts while evolving to a larger body size—providing that stylet feeding led to tapping adequate food sources along the way. It did, and yielded a variety of Homoptera in the Permian and the Heteroptera later on.

There are several hints that the Hemiptera were originally smaller than most are today. They are usually thought to have evolved from a psocopteroïd ancestor, and the Psocoptera are small. The Sternorrhyncha are small. The hemipteran antennae are comparatively short and usually have few segments, and the tarsi have fewer than the primitive five segments.

In *Scutigera* (Chilopoda), and presumably elsewhere, long antennae are important in sensing a leg track and the many-segmented tarsi (with claws) are important as automatic grappling devices in species which run too fast to select footholds (Manton, 1952). In very small individuals a secure foothold is usually more advantageous than running speed, and species of small body size have often lost tarsal segments and antennal length.

Many Hemiptera or Homoptera have reattained a larger body size and have acquired additional means for avoiding their predators. The Auchenorrhyncha, for example, are able to jump, or they live beneath the ground surface (cicadas).

Example 6.—The implications for the Pterygota are somewhat different than for primitively wingless tracheates, since the winged adults would conceivably fly to escape; their immature stages could not. Accordingly, we should postulate that, 1) extinct pterygote orders characteristically had exposed, terrestrial immatures that were especially susceptible to tetrapod predation, and 2) the immature stages of surviving orders will have effective means for avoiding visually-hunting tetrapod predators.

Both predictions are fulfilled among Palaeoptera: the only surviving orders are the Ephemeroptera and Odonata, and both have aquatic immature stages. Some fossils indicate that the Paleozoic Ephemeroptera were also aquatic (Hubbard and Kukalova-Peck, 1980). The aquatic habits of these orders effectively removed their immature stages from terrestrial reptile predators.

But would an aquatic life secure the im-

matures from vertebrate predation? Fish, many of which would eat insects, were already present, and would not the amphibians and littoral reptiles pursue insects into the water?

The answer is that pterygote insects had two significant advantages: they were smaller, and their adults flew. Flight enabled the adults to colonize smaller, less permanent and more widely scattered bodies of water. Their larvae would be able to utilize food in bodies of water or portions of them not suitable for or even accessible to fish or any vertebrate specialized for an aquatic mode of life. The small size of these insects enabled more individuals per body of water (for a given productivity), and, hence, relatively larger breeding populations and a relatively larger probability of at least some adults finding another body of water. The early aquatic paleopterans retained their evolutionary potential because of the size of their breeding populations and adult migrations.

While not paleopterous, the Plecoptera also appear to have survived the Paleozoic because their immature stages had become adapted to living in water beyond reach of tetrapod predators.

The paleopterous orders that became extinct would be expected to have had terrestrial immature stages. This is suggested by the long ovipositors of many of these species (Carpenter, 1971), that usually correlate with oviposition in soil, various crevices, or plant tissues rather than in water. Fossil immatures are very scarce for these groups, which is probably a consequence of terrestrial habits that seldom placed them in sites suitable for fossilization (Lemche, 1940). No immatures of these orders have been found yet that exhibit aquatic adaptations, and convincing information has been accumulating to show that the immature stages of at least some Palaeodictyoptera and Megasecoptera were terrestrial (Lemche, 1940; Carpenter, 1977; Carpenter and Richardson, 1971; Wootton, 1972).

Carpenter and Richardson (1968) men-

tion some crucial information: the later instars of the Paleozoic Megasecoptera and Palaeodictyoptera had large, posterolaterally projecting wing pads. It is these large, developing wings that would cause serious problems in avoiding vertebrate predators. In immatures not yet able to fly, large pads would interfere with burrowing into ground litter or entering crevices to hide. These immatures must have been easy prey for arthropod-eating reptiles; it is not surprising that they became extinct.

Carpenter (1977) thought that the Protodonata must have been aquatic, apparently because they are so similar to the Odonata, as he had mentioned earlier (1947). However, he also mentioned (1947) that August Krogh had stated that the immature stages of the giant meganeurids would have been unable to respire via caudal tracheal or rectal gills. The vertebrate predation hypotheses developed here, are in accord with Krogh's statement, and it seems much more likely that the Protodonata were simply the terrestrial branch of the Odonata. They became extinct because their immature stages were exposed on the ground where they were vulnerable to vertebrate predators, although it may be that their early instars were passed in water. Their near-adult immatures may have been sufficiently large to resist many tetrapod predators.

The Paleoptera did not originate as aquatic animals. Both adults and immature stages (Odonata and Ephemeroptera) are abundantly supplied with tracheae that belie their terrestrial origins. The idea that wings originated as aquatic adaptations is beset with serious weaknesses, inasmuch as movement in water and in air would impose vastly different demands on lateral flaps. Moreover, at least some Paleoptera were clearly not aquatic as immatures, as already mentioned. The immatures of the Odonata evidently became aquatic independently of the Ephemeroptera, since the immatures of the two have developed different respiratory adaptations for their aquatic lives.

In general, Ephemeroptera show more

primitive features than Odonata, and their gill covers seem to be serially homologous with wings (see Kukalova-Peck, 1978). However, gill covers may just as easily be adaptations of preexisting lateral flaps (whatever their origin) to an aquatic life as new structures resulting from selection in an aquatic environment.

Since there is no very feasible pathway from an epiphytic mode of life to an aquatic one, the Odonata and Ephemeroptera are necessarily interpreted as remnants of lineages that originally lived on the ground surface. Their terrestrial relatives are all now extinct.

Several endopterygotes (Neuroptera, Mecoptera, Trichoptera, and Coleoptera) appear in Lower Permian deposits (Carpenter, 1977). Odonata appear about the same time. The Ephemeroptera appear in the Carboniferous as only a single species, but they became abundant in the Permian. The Palaeodictyoptera show the reverse pattern of many species in the Carboniferous, but only a sparse representation in the Permian (Carpenter, 1976). These data suggest that vertebrate predation on the ground became critical about the time of the Carboniferous-Permian transition, that is, about the time that the reptiles began their first explosive adaptive radiation. The data are also consistent with the idea that some species, in this case the few Permian Palaeodictyoptera, may have survived in arboreal refugia until reptiles became efficient climbers.

Example 7.—Endopterygotes evolved from species in which the immature stages had entered the soil litter. Projecting wing pads impede back-and-forth maneuverings in subsurface environments, and were selected against in burrowing pterygote immatures; the endopterygote condition is thus a result of entry upon a burrowing life (Hinton, 1948, 1977). It is also a result of selection by visually hunting vertebrate predators (the two ideas are compatible). Tetrapod predators eliminated groups that had immature stages exposed on the surface of the ground.

Hennig (1981, p. 278) objected to Hinton's views, and asserted that thysanuroid or campodeiform larvae were primitive for endopterygotes, and that these were not suited for burrowing in firm substrates. Hence, the endopterygote condition arose for reasons other than as an adaptation for burrowing life: it may have contributed to the subsequent evolution of endopterygotes but not to their origin. However, it is unlikely that Hinton implied anything more in his general statement than that the endopterygote condition resulted from selection in a subsurface environment. Obviously, the first larvae could not have been very different from the immatures of other insects. They did not begin as burrowers in plant tissues or firm soil; they merely entered spaces in the ground litter. A thysanuriform larva, as occurs in many neuropteroid insects, is a reasonable model for an early endopterygote larva, as Hennig noted and as Hinton probably implied.

Because about 88% of all insects are endopterygotes (Hinton, 1977) it has often been assumed that the internalization of the developing wings in endopterygote larvae preadapted them to invade environments not available to immatures with external wing pads (see Hinton, 1948, 1963, 1977; Hennig, 1981; Clements, 1968). For the first time the distributive and reproductive adult stage was completely dissociated from the feeding larval stages. According to this view, the adult-larval dissociation conferred advantages in utilizing a new, hidden type of food from which the less-suited exopterygote immatures were excluded (Hinton, 1977). This implies that selection was basically for an ability to obtain hidden, larval foods by burrowing, while the adults could still disperse. Once larvae had gained effective access to such foods they underwent a major adaptive radiation on them.

The hypotheses developed here require that these ideas be modified. Visually hunting, terrestrial vertebrate predators selected severely against species that had surface-dwelling immature stages. Endopterygote

larvae were not affected, since they lived out of sight under litter, and their adults probably spent much of their time up on vegetation out of reach of early tetrapod predators.

The ensuing adaptive radiation of endopterygotes occurred in groups having larvae that lived in litter—to which they were limited during the day by the larger tetrapod predators. It did not occur because larvae gained sudden access to a previously untapped, major food resource. That would have been reflected in a sudden "explosion" of the endopterygotes. The radiations occurred over a longer period of time because the increasing complexity of land environments provided more hidden "niches" into which endopterygote larvae could move from time to time. The adaptive radiations of the angiosperms appear to have resulted in the greatest complexity and the most niches for endopterygote larvae. There is no reason to assume that there were fewer exposed niches for exopterygotes. Exopterygotes have been unable to radiate freely in exposed niches since the end of the Paleozoic because of the ever-present vertebrate predators.

The divergence of the Endopterygota into the neuropteroid and mecopteroid orders seems to have been initiated by comparatively simple specializations for two divergent modes of larval life. Mecopteroïd larvae found food in the soil and fed there day or night out of sight of potential vertebrate predators. The neuropteroids hid in soil litter during the day, but emerged to forage at night. The nocturnal wanderings of some early neuropteroid larvae led them into crevices beneath bark where they found an ample supply of fungi. Their adults could enter the same crevices, and these became the Coleoptera.

The longer antennae and legs of the larvae of primitive Neuroptera (*sensu lato*) and Coleoptera at first appear somewhat incongruous with the invaginated wing pads and lack of compound eyes (the first suggest an

active life on surfaces, the second a burrowing mode of life). These are, however, just the features required for insects that burrow during the day but forage over surfaces at night. The wandering habit also explains how the Neuroptera got to their extremely diverse larval habitats (in water, soil, under bark, stones, on plants). Mecopteroïd larvae did not leave the soil to wander at night, and became more worm-like as befits a burrowing mode of life and, accordingly, developed very short antennae and legs. The mecopteroid adults could not remain exposed near their underground larvae because of vertebrate predators, nor could they specialize like their larvae for burrowing, since that would require sacrificing the adult adaptations for flight and dispersal. In this sense vertebrate predators coerced the adult-larval dissociation of endopterygotes. More accurately, they ate the comparatively vulnerable surface-dwellers out of existence, leaving behind larval burrowers that had arboreal and aerial adults. Before the advent of reptiles, such species would probably have appeared as minor evolutionary side issues.

Example 8.—Neoptera are able to flex their wings backward over or alongside their abdomens when not flying. The flexing mechanism originated very early in the evolution of insects. It was present among the first known winged insects of the Carboniferous (Carpenter, 1977; Kukalova-Peck, 1978; Rolfe, 1980). That vertebrate predators were involved in selecting for the wing-flexing mechanism is at least implied by statements that it enabled winged adults to enter crevices and hide (Carpenter, 1977; Kukalova-Peck, 1978; and others). Presumably, they hid from their larger tetrapod predators.

Some authors mention that flexing the wings backwards would facilitate crawling through vegetation with less risk of damage to the wings (Kukalova-Peck, 1978; and others). If so, the greater facility in moving through vegetation might also be related, at least in part, to predator escape. Wootton

(1981) suggested that the ability to flex the wings backwards provided three advantages for Paleozoic insects: it enabled a greater mobility with less risk of wing damage, as just mentioned; it reduced their wind resistance and the likelihood of the insect being blown off vegetation; and it enabled the adults to enter crevices.

Neither mayflies nor dragonflies have moved toward a wing-flexing mechanism even though they typically perch in exposed sites that would seem to render them especially vulnerable to wind gusts. Damselflies ordinarily operate in less exposed habitats where winds are seldom a problem. Yet, it is they that are characterized by an analog of the wing-flexing mechanism. Their thorax is so extremely tilted that the wings extend backwards over the abdomen even though they are only simply folded dorsally from a morphological perspective. Winds would seem to be among the less plausible agents selecting for a wing-flexing mechanism, but there is no very obvious way to assess earlier roles of wind selection.

There is some evidence for believing that mobility in vegetation was important; ant and termite adults discard or chew off their wings once they have completed their nuptial flight—that is, after the wings are no longer needed.

There are two difficulties to be resolved if neoptery is to be explained as a consequence of entering crevices.

Difficulty 1. The first Neoptera could fly. If so, for what reason would winged insects that could fly to escape predators resort to hiding in crevices? Theoretically, flight should have been a most effective means of escape, and the large wings would certainly cause major problems in entering crevices.

This difficulty results from an uncritical extrapolation from too simple a basis. The early Neoptera were very primitive insects. They had essentially no metamorphosis (Kukalova-Peck, 1978). A distinct metamorphosis, as characterizes most modern winged insects, may not have developed ful-

ly until after the Paleozoic (Kukalova-Peck, 1978). The primitive adults developed only gradually from immature stages from which they probably differed little in either morphology or mode of life.

In this light, entering crevices would presumably have been one of the most immediately available means for escaping vertebrate predators. It would not require new behavior patterns, since even before wings arthropods must have entered crevices regularly to avoid desiccation during dry periods. The arthropods could remain in the crevices during the day, but emerge to feed at night when vertebrates would be unable to see and pursue them effectively.

Since their development was so simple, basic escape patterns would necessarily be carried from instar to instar. But, since there was no significant metamorphosis, the escape patterns of the immatures would almost certainly be carried into adulthood. This is consistent with Kukalova-Peck's idea (1978) that neoptery, among other events, developed first in the immature stages, although, strictly speaking, the changes would have developed simultaneously in both immature and adult stages. It is not unreasonable that the adults should escape via the same means as their immatures, particularly in primitive insects. It is still the rule in the jumping Collembola, Saltatoria, or Homoptera, in the cryptically colored orthopteroid insects, or in Blattodea—essentially all insects that have not developed widely divergent adult and immature modes of life.

Difficulty 2. Neoptera appear to have differentiated along two incompatible lines, with but few persisting, undifferentiated relicts. The Blattodea exemplify one type. These are fitted characteristically, and no doubt primitively, for a life in crevices, such as under the bark of trees. In such confined spaces the wings are subject to abrasion, and the front wings became thickened, protective covers for the hind wings. The prothorax is also characteristically and primitively rather loosely joined to the

mesothorax in these insects, probably because in shifting the burden of flight to the metathorax there was no longer any great need for a large, fixed phragma between the pro- and mesothorax for the attachment of the mesothoracic, indirect flight muscles.

A second type of Neoptera relies primarily on the mesothorax rather than the metathorax for flight. The prothorax is always more or less fused with the mesothorax in these groups, because in this case a well-developed phragma between these segments is essential for the operation of the indirect flight muscles. If a pair of wings is modified, it is the hind pair, principally by reduction, as in Diptera or Hymenoptera. But these Neoptera never show any hint of thickened mesothoracic wings, nor does their behavior suggest that they ever lived in crevices.

Thus the difficulty: "crevice-entering" behavior that resulted in thickened front wings seems to have affected the evolution of only some Neoptera and only after the wing-flexing mechanism had already originated, apparently for reasons other than entering crevices.

The hypothesis consistent with the most data is that the wing-flexing mechanism first evolved as a facet of "crevice-settling" behavior, in which the winged adult simply settled into open crevices in bark or on the ground. Since they were only partly concealed, immobility during the day would be almost essential to the behavior. Even if crevice-settling insects were not completely concealed from view, it would not be easy for a much larger vertebrate to remove them from small crevices. Perhaps more crucial, especially on trees, settling into crevices and flexing the wings back along the abdomen eliminated the silhouette that otherwise would so readily disclose the insect's position to potential tetrapod predators.

One reason for thinking that crevice-settling rather than running through vegetation was the more significant feature of early winged insects is that crevice-inhabiting in-

sects appear to have supported major adaptive radiations among beaked birds and perhaps the pterodactyls earlier. The loss of teeth and development of a relatively long beak are adaptations for fishing insects out of crevices. The beak developed in winged animals, as would be expected: the ability to move from tree to tree (or from stand to stand) would be essential for survival, since single trunk surfaces would not ordinarily support sufficiently large insect populations for predators as large as birds or pterodactyls. Insectivores, such as bats, shrews, and lizards, that do not pick their prey from crevices, have not developed beaks.

#### THE PROBLEM WITH FLYING DURING THE DAY

By and large the neopterous orders seem primitively to have had nocturnal adults. Many adults are still nocturnal. In general, these are singularly reluctant to fly to escape diurnal predators. Modern representatives most often rely primarily on physical concealment, cryptic coloration, or means other than flight to escape diurnal predators, as in moths or Trichoptera that are concealed by their coloration on tree bark, or in Blattodea, Coleoptera or Dermaptera that seem primitively to have hidden in crevices with their immatures.

This reluctance to fly (during the day) is understandably adaptive in modern environments. To fly out in the open in the day is to be conspicuous and to risk capture by birds. However, the basic nocturnal patterns for all these orders appear to be very ancient; they were laid down long before birds evolved.

This is not so puzzling as it might seem. While not often considered in this regard, modern Odonata are significant aerial predators. In the tropics they are evidently more effective than birds in excluding Ephemeroptera from diurnal activity over the streams in which they breed (Edmunds and Edmunds, 1980). Presumably, the Protodo-

nata earlier augmented the depredations of the Odonata. Insects flying or swarming during the day would be conspicuous targets for such aerial predators. This surely accounts for the early avoidance of diurnal flight in many insects.

Of course, flight is also costly in terms of energy, an added reason to depend first on means other than energy-expensive flight for escaping predators. Nevertheless, the Odonata, Ephemeroptera and Diptera seem to have been fundamentally diurnal and aerially oriented.

The Odonata and Ephemeroptera have short, setaceous antennae. They do not feel the substrate with them as they move about at night (they do not seem to walk much at all). Diptera have also repeatedly developed comparable antennae (stylate and aristate types), and they do not use them to test the substrate like Blattodea or other active nocturnal insects. Most Diptera also fly readily to escape during the day.

Many Ephemeroptera swarm at dusk or at night, although, like the diptera, they do so at visual markers, which betrays their earlier diurnal orientation. The nocturnal habits of tropical species at sites remote from breeding sources (Edmunds and Edmunds, 1980) are probably the extreme effects of severe selection pressure on primitively diurnal insects. They have obviously not been able to cope well as adults, and have survived mainly because of advantages their immature stages developed in their long history in aquatic environments. Their lack of a wing-flexing mechanism prevents practical crevice-entering behavior, and it reduces the effectiveness of cryptic coloration because of their conspicuous silhouette.

As developed elsewhere (Downes and Dahlem, 1987), the labellum of Diptera gave flies early access to sugar fuels in the thin, dried films of Homoptera honeydews. Diptera alone among insects had consistent effective access to naturally occurring sugars until flowers appeared in the Cretaceous.

Thus, they almost alone among insects could afford the high cost of flight, or, perhaps, the cost of flight swift enough to evade early odonate predators.

The early endopterygote adults probably spent much of their lives on trees. As reptiles became efficient climbers, the endopterygotes could respond to this new threat in several ways. They might become very small so as to become unattractive as prey. This is not a practical response for endopterygotes, since moving from their larval life in litter or soil to an adult life on tree trunks would present major transportation difficulties for such small insects. Only the exopterygote Psocoptera, in which both immatures and adults live together on tree trunks, appear to have pursued this option.

Visually hunting vertebrates must often have selected continuously for another response—better cryptic coloration—as seems to have developed in Trichoptera or Lepidoptera. Another possibility would be for the adults to move out to the tips of branches where the heavier vertebrates would have difficulty in pursuing them. The Diptera seem to have taken this tactic, and it is one that would be more likely to place them on leaf surfaces bearing honeydew than the alternative of hiding in crevices on trunks. Crevice-settling would not be possible at branch tips, and this may have contributed to the dipteran tendency to remain basically aerial in their orientation.

#### CONCLUSIONS

Vertebrate predators brought about the extinction of several major arthropod types near the close of the Paleozoic. They were major shapers of the conspicuous adaptive features of every major surviving terrestrial arthropod group. They indirectly account for the adaptive radiation of Endopterygota, simply because they inhibited the adaptive radiations of related groups having comparatively exposed immature stages.

For adults, flight would seem to be a first

choice and the most effective means of escaping tetrapod predators. It may have been an effective escape in the earliest Pterygota, but by the Permian winged insects that flew to escape tetrapod predators risked capture by Odonata or Protodonata. For this reason most adult Pterygota opted for various alternatives to flight as their primary means for escaping tetrapod predators. In many an escape response of the immatures was carried into adulthood, and adults and immatures pursued similar lives in the same concealed places.

The Neoptera simply continued a very elementary escape pattern of their immatures; they settled into open crevices. The ability to flex their wings backwards enabled them to enter crevices, and flexing served the larger immatures as well as the adults. The flexing mechanism also eliminated the insect's characteristic silhouette that so readily gave away its position. Elytra and thickened front wings developed after some winged Neoptera joined their immature stages in larger crevices out of sight of tetrapod predators, at least during the day.

Odonate adults continued to escape tetrapod predators by flying; but they were the aerial predators, and they have remained strong fliers. Because they could not flex their wings, the Ephemeroptera adults could not settle into or enter crevices as Neoptera, nor could they join their aquatic immatures. Flight seems to have remained as their principle means of escape, but they have survived mainly on the strengths of their immature stages in aquatic environments.

The Diptera are the third surviving order in which the adults have retained an essentially aerial orientation. They evidently left their original crevice-settling behavior very early in their evolution to assume a more thoroughly aerial life as they gained access to the sugar-fuels of Homoptera honeydew. They do not seem to be derived from stock that had nocturnal adults. Their early access to fuels enabled a faster flight, and their halteres probably conferred an agility that al-

lowed them to fly more freely during the day with less risk of capture than in other Pterygota. Efficient modern predators, such as birds or Odonata, have probably selected for the nocturnal or crepuscular habits of certain groups, although many "lower" Diptera still swarm in the open during the day, at least in temperate regions.

Their small size rendered Collembola and Psocoptera unattractive as prey for most tetrapod predators.

Only a few of the implications of tetrapod-predation hypothesis are developed above. Thus far, all fit available observational data. No other hypotheses about the major features of terrestrial arthropod evolution currently account for such a wide variety of observational data.

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